XXVIII.—*On the Pterylography of the Hoatzin,* Opisthocomus cristatus.

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(Plates IX.–XI.)

Although several writers have recorded observations on the pterylography of *Opisthocomus,* no one hitherto has given a really complete account of the pterylosis either of the adult or of the earlier stages. So far as the material which has been submitted to me has permitted, I have endeavoured to fill this gap, and trust I shall be found to have succeeded. Certain points relative to the development of the neossoptiles and embryonic rhamphotheca (p. 352) are yet under investigation; but these belong rather to the province of histology than pterylography, and will be treated of in a future paper, together with a few details concerning certain muscles which I have studied.

My investigations have been carried on in the Department of Comparative Anatomy of the Oxford University Museum, and hence have been subject to the control of Prof. E. Ray Lankester, to whom I wish to express my thanks for grants of time from other work, and for other favours.

I propose to proceed with my description from the known to the unknown, from the adult to the embryo.

I. *Pterylosis of the adult* Opisthocomus.

Pterylæ:—

Pteryla capitis (Pl. IX. fig. 1, *Pt.cap.*).—Of the feathers of this tract on the sides of the face nothing remains but a few bristles, which represent the shafts of sometime feathers. The eyelids are provided with eyelashes.

*Pt. colli** (Pl. IX. figs. 1–3, *Pt.coll.*).—This is a con-

* Usually the neck-tract is divided into a dorsal and a ventral band by an apterium—the apt. colli laterale. Sometimes, by a forward extension of the *apterium mesogastræi* and *spinale,* the neck-tract is divided not into a dorsal and ventral, but two lateral tracts—the *pterylæ colli laterales* of Nitzsch.

I propose now to restrict the term *pt. colli* to those cases in which the

tinuous tract, more or less completely investing the neck. There is a distinct tendency to form a *pt. colli dorsalis* and *pt. colli ventralis* (see footnote), in that the feathers in the mid-dorsal line stand closer together than on the sides of the neck, in which region they are somewhat sparsely distributed, thus suggesting an incipient differentiation into the usual dorsal and ventral tracts (see footnote).

Pt. ventralis (Pl. IX. figs. 2, 3, *Pt.v.*).—This tract completely invests the whole of the upper part of the breast, rather below the middle of this region; that is to say, a short distance above the sternal callosity (p. 352) it divides into two widely separate and very narrow branches, which, gradually expanding, terminate a short distance in front of the cloacal aperture. This tract is noticeable throughout for the sparseness with which the feathers are distributed.

Pt. ani (Pl. IX. figs. 2, 3, *Pt.a.*).—A circlet of small feathers surrounding the cloacal aperture.

Pt. humeralis (Pl. IX. fig. 1, *Pt.h.*).—A clearly defined, though small and slightly developed, tract of some two or three feathers in width. The constituent feathers are but slightly stouter than those of the *pt. spinalis* running down beside it, but they are very long, the most posterior and longest reaching nearly down to the tail. Passing forwards and downwards this tract is lost in the upper portion of the pt. ventralis.

Pt. femoralis (Pl. IX. figs. 1–3, *Pt.f.*). The feathers of this tract are very long and sparsely distributed; it is connected both with the *pt. spinalis* and *pt. cruralis*.

Pt. cruralis (Pl. IX. figs. 1–3, *Pt.cr.*).—This tract is com-

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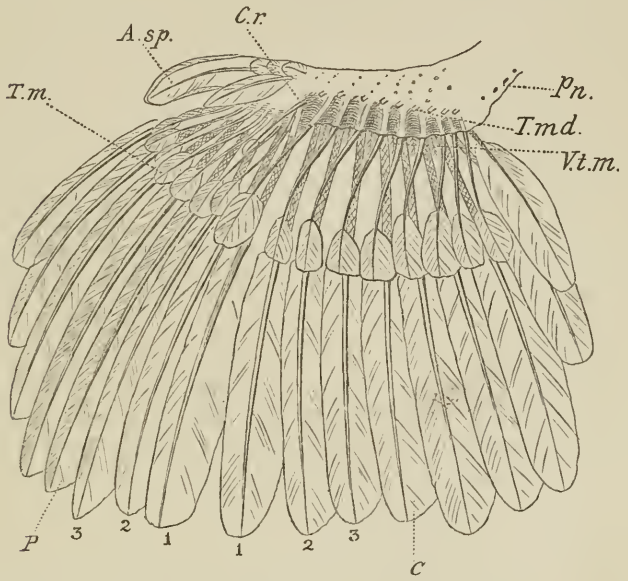
neck-tract is continuous; when, as in the typical arrangement, the tract is divided into a dorsal and a ventral band, I would distinguish the former as the *pt. colli dorsalis* and the latter as the *pt. colli ventralis*.

Pt. colli is a new name recently adopted by Dr. Gadow in Prof. Newton's 'Dictionary of Birds,' and should be gratefully welcomed. Up to the present the neck-tracts have been described simply as the dorsal and ventral moieties of the spinal and ventral tracts; although this system was perfectly correct, yet, as those who speak from practical experience know, it was not always convenient.

posed of long and fairly well-developed feathers; on the inside of the leg they are smaller and have a discontinuous vexillum.

Pt. uropygii (Pl. IX. figs. 1, 3, *Pt.u.*).—A large, thick, brush-like tuft of downy feathers surmounts the oil-gland,

Fig. 1.



Wing of *Opisthocomus*, extended.

Left wing of *Opisthocomus* (adult), showing the form when fully extended. The proximal portion of the vane of the remiges and major coverts has been removed. *A.sp.* Ala spuria; *C.r.* Carpal remex; *C.* Cubitals; *T.m.* Tectrices majores; *V.t.m.* Ventral tectrices majores; *T.md.* Tectrices mediæ (cut short); *Pn.* Parapteron; *P.* Primaries (metacarpo-digitals).

whilst its base is encircled by a ring of down-feathers having a large aftershaft.

Pt. alaris (woodcut, fig. 1).—Remiges:—Metacarpo-digitals (primaries) 10. Cubitals (secondaries) 11. Quintocubital.

As will be seen in the figure, the remiges are of great length relatively to the length of the limb; the longest remex of both

primary and cubital series is almost twice the combined length of the manus and forearm. The metacarpo-digital remiges are not separated from the cubital series by a diastema, as is usual, but are closely approximated, the space between the two series being about equal to that dividing any two "metacarpals." In other birds the "carpal diastema," as I propose to call it, is considerable—rarely less than the space dividing any two of the cubital remiges, which are always the more widely spaced. This crowding of the two series of remiges seems to be correlated with low powers of flight.

Of the cubital remiges it is interesting to remark that usually one finds they are separated by fairly uniform spaces, —decreasing proximally—whilst here the space dividing Nos. 1 and 2 is less than the similar space separating each of the remiges from 2–5, where the spaces appear to be rather above what I should be inclined to fix as the normal width.

Tectrices :—

T. majores (woodcut, fig. 1, p. 347, *T.m.*).—Usually the major coverts on the dorsal surface of the manus are as perfectly developed as those on the cubitus; in *Opisthocomus*, however, it will be noticed that the feathers of this region are much smaller than the cubital coverts. This is an arrangement which occurs but seldom. I find it to obtain in such forms, for instance, as *Psophia*, *Dicholophus*, and *Musophaga*. Although possibly of no great significance, this is an interesting fact.

On the ventral surface this series is throughout reduced to relatively small discontinuous feathers with a degenerate hyporhachis (fig. 1, *V.t.m.*).

T. mediæ (woodcut, fig. 1, p. 347, *T.md.*).—The cubital coverts of this series on the dorsal surface increase in length from without inwards, so that the most proximal feathers are more than half as long as the major coverts underlying them.

On the manus Nos. 1–4 are absent, as is often the case with other birds; the remainder of the series is fairly well developed.

On the ventral surface this series is represented only on

the cubitus, where they appear as very small discontinuous feathers, with a degenerate hyporhachis.

T. minores.—On the dorsal surface, commencing in the carpal region with two rows, an additional row is added proximally, owing to the increased space afforded by the muscular surface of the forearm and patagium. They may be described as relatively long feathers. Proximally the last row (pre-axial) is continued for a short distance on to the arm. This series is absent on the hand.

On the ventral surface there are two cubital rows, widely separated; the second is continued over on to the manus. A third row is indicated by the presence of some two or three feathers along the pre-axial border of the muscles of the forearm.

T. marginales.—There are three cubital rows of this series. Examined from the pre-axial margin of the wing backwards, these rows will be found to become somewhat closely approximated in a direction transversely to the main axis of the wing; thus groups of three are formed; between each two such groups a considerable diastema intervenes, interrupted only by a feather in the extreme pre-axial margin in the middle of the diastema; this feather is longer than its fellow on either side. This arrangement is expressed by the accompanying dots (⋮˙⋮). A similar arrangement obtains in most birds, but the rows (transverse) are much more numerous and so closely crowded as to render a correct interpretation difficult. This series connects the pt. alaris with the pt. ventralis, and distally clothes the extreme pre-axial border of the manus.

On the ventral surface there are three rows of these coverts, of which two run along the extreme pre-axial border of the cubitus, whilst the third is placed a little further back; the first row is longer, and the second shorter, than is normally the case in other forms.

Ala spuria (woodcut, fig. 1, p. 347, *A.sp.*).—The ala spuria is composed of four large "remiges," almost equalling in length the t. majores of the cubitus.

Carpal remex (woodcut, fig. 1, p. 347, *C.r.*).—On the

whole I am inclined to regard this feather as the "remex," and not the "covert" of Degen (2). It is rooted in the very small carpal diastema at the base of the first metacarpal remex, and is a relatively large and well-developed feather, being about as long as the cubital t. mediæ.

Parapteron (woodcut, fig. 1, p. 347, *Pn.*).—The parapteron is composed of two rows of feathers, which, as usual, seem to be serial with the t. majores and t. mediæ. The feathers along the post-axial margin are the longest. The third row of smaller feathers intercalcated between the post-axial rows appears to be wanting.

Hypopteron (Pl. IX. fig. 3, *H.*).—Represented by five moderately long and somewhat semiplumous feathers arising over the region of the dorsal border of the pectoral muscles, and extending outwards on to the arm running along the post-axial border, and not forward, as usual.

Apteria:—

Apterium capitis (Pl. IX. fig. 1, *Apt.cap.*).—Represented by a large space embracing almost the whole side of the head, and is apparently of a light blue colour in life. The surface of this space is broken up by the bristles previously referred to, running down in front of and beneath the eye, a few feathers round the opening of the external ear, and a small patch of feathers between that orifice and the rhamphotheca of the mandible.

Apt. spinale (Pl. IX. fig. 1, *Apt.sp.*).—Extends from between the shoulders to the region just above the posterior border of the ilium.

Apt. trunci laterale (Pl. IX. figs. 1–3, *Apt.t.lat.*).—Arising from the same region as the spinal apterium, from which it is divided only by a narrow strip of the pt. spinalis, it extends backwards to the femoral tract; expanding meanwhile downwards, it embraces almost the whole side of the body.

Apt. mesogastræi (Pl. IX. figs. 2, 3, *Apt.m.*).—A somewhat pyriform space extending from the region rather below the middle of the breast to the cloacal aperture.

Apt. alæ superioris (Pl. IX. fig. 1, *Apt.a.sup.*).—The small space dividing the humeral from the wing-tract.

Apt. alæ inferioris (Pl. IX. fig. 3, *Apt.a.inf.*).—Embraces the pre-axial border of the ventral surface of the arm and patagium.

Down-feathers :—

These are distributed sparsely over the whole body; but on the head and upper part of the neck they are reduced to the verge of extinction. On the trunk they are very long, and more or less definitely arranged, so as to run in double rows between two rows of contour-feathers (see Pl. X. figs. 2, 3, indicated by small dots). This rule, however, is by no means strictly adhered to, since it often happens that down-feathers intrude themselves between contour-feathers, *i. e.* run transversely to the general parallel lines.

Pulviplumes or *Powder-down*.—Absent.

Filoplumæ.—One at the base, and to the outer side, of every contour-feather. They are about half as long as their respective contour-feathers, have a black shaft and light yellow vexillum. Those accompanying the remiges are rather larger and have a considerable vexillum.

Structure of the Contour-feathers.—A noticeable feature about the contour-feathers is their fewness and relatively great length throughout the whole body. The individual feathers preserve their pennaceous structure throughout to a singular degree, inasmuch as the rami at the base of the contour-feathers usually become more or less downy, whilst here only the extreme edge of the vane or vexillum takes on this downy structure.

The aftershaft, though nearly half as long as the main feather, has a short and very slender axis, bearing a few long and delicate rami, the radii presenting the appearance of minute setæ along the shaft of the ramus. In the feathers on the head the transition from contour-feathers to simple bristles can be traced by a series of most perfect gradations.

Structure of the Plumulæ.—The down-feathers form large brush-like tufts, and possess both rhachis and aftershaft, which is of considerable size. Microscopically the radii, like the neossoptiles, have well-developed fila; in this they differ from the nestling plumulæ, in which fila are rare.

Rhamphotheca.—Simple. Nostrils impervious, nearer the base than the tip, and having a comparatively large, oval, unprotected orifice. Along the rhamphotheca of both upper and lower jaws, on the inner side, a little removed from the tomium, there runs a short ridge extending from the back of the mouth forwards to a point corresponding with the anterior margin of the external nares; this ridge supports a row of horny cones, which are probably used for crushing the fruit on which the bird largely lives*.

Podotheca.—Scales on the acrotarsium large, reticulate, on the acropodium shield-shaped. Planta granulated.

Claws on the wing absent, on the feet moderately large.

Sternal callosity.—This is an elliptical horny patch of skin lying immediately over the sternal keel, and is apparently due to the fact that this part of the body is applied to the branch upon which the bird is resting: as will be seen in Pl. IX. fig. 3 (*St.cal.*), it is placed obliquely to the long axis of the trunk, hence is well adapted for this purpose. Such a horny pad is rare amongst birds; the Rhea and Ostrich may be quoted as examples in which it occurs.

Moulting.—According to Mr. Quelch (11) there is no periodic moulting-season, but the feathers are renewed fitfully: that is to say, moulting goes on all the year round.

II. *Pterylosis of the Nestlings of* Opisthocomus.
(Pl. X. figs. 1–3.)

There are five nestlings exhibiting as many gradations in the development of the plumage; I shall therefore describe them in five stages, remarking, however, only such particulars as are of any importance.

Pterylæ.—So far as the distribution of the feathers is concerned, a reference to the Plate will show that the pterylosis of the nestling differs from that of the adult chiefly in that the pteryla ventralis is continuous as far as the sternal

* I have purposely deferred a more careful description until I have made a thorough examination of the rhamphotheca in all stages of development.

callosity, instead of dividing at some distance in front of this point.

The mode and rate of development of the nestling-plumage reveals some points of considerable interest.

In stage 1 (Pl. X. figs. 1–3) the body is but scantily clothed by the neossoptiles*; between these, minute specks, arranged more or less definitely in rows, can be seen; these are the tips of developing plumulæ or down-feathers, concerning which we shall have more to say later.

Pt. alaris (Pl. XI. fig. 2).—Here it will be noticed that the remiges are just beginning to make their appearance, bearing out the neossoptiles on their tips. The proximal primaries are furthest developed; the proximal cubitals are indicated by neossoptiles.

T. majores.—These are, as yet, only represented by neossoptiles above their respective remiges. The remaining tectrices are represented by the tips of the neossoptiles breaking through the skin.

Stage 2. The plumulæ have increased in size so as to appear like little brush-like tufts; but on the head and back part of neck they remain much as in stage 1.

Pt. alaris:—

Primaries.—These have now pushed their way out a considerable distance beyond the wing, the individual remiges preserving the same relative lengths as in stage 1; remex 10, however, must be excepted, inasmuch as nothing but the neossoptiles can be seen.

Cubitals.—Preserve the same relative length as in stage 1; the proximal remiges are as yet only indicated by neossoptiles.

Tectrices:—

T. majores.—The definitive feathers on the dorsal surface of this series are now making their appearance. The remainder of the coverts are as yet only represented by neossoptiles. The under surface of the wing appears as though

* For the origin and meaning of this term see 'Dictionary of Birds,' Newton, Article "Feathers," p. 243.

sparsely besprinkled with minute down-tufts, more or less definitely arranged, and indicating the definitive feathers.

Stage 3. The true down-feathers (plumulæ) have still further increased, save those on the head and neck, which still remain undeveloped.

Pt. alaris :—

Primaries.—The vanes of these feathers are beginning to unfold, and have considerably increased in length. The sheath enveloping the vane of remex 10 is just appearing.

Cubitals.—The development of these remiges decreases from without inwards. Thus, while No. 1 is about as long as the major covert of the hand, or, in other words, is about half an inch long, No. 10 is as yet only represented by its neossoptile.

Tectrices :—

T. majores.—Those on the hand rather more than half as long as primaries; the vane is just beginning to burst through its enveloping sheath.

On the cubitus they are much further developed than their respective remiges, so that they appear rather as remiges than coverst. Like the remiges, they decrease in length from without inwards, so that only a small portion of the vane of the most proximal covert has yet appeared.

T. mediæ.—The definitive feathers of Nos. 1–3 have just begun to make their appearance.

Under surface of wing as in stage 2.

Stage 4. The function of the neossoptiles is on the wane, inasmuch as they now appear borne out upon the pencil-like* tips of the definitive feathers.

The true down-feathers (plumulæ) have greatly increased, so as to almost entirely conceal the skin; on the back part of the head and neck, however, their development is very slight.

Pt. alaris :—

Primaries.—These have greatly increased in length.

* The vanes of the definitive feathers, at a certain stage of development, resemble a camel-hair pencil brought to a fine point.

Cubitals.—The proximal remiges still remain undeveloped, being only represented by the neossoptiles.

The contour of the wing has now changed, and the post-axial margin has extended backwards towards the free finger-tip; this will be seen better in stage 5.

Stage 5. The plumage is now made up partly of the pencil-like tips of the definitive feathers, and the neossoptiles, attached to their tips, and partly of plumulæ, which have now attained considerable size. The neck, however, is still but sparsely clothed. The down-feathers remain at about the same grade of development as in stage 1.

Pt. alaris (Pl. XI. fig. 3) :—

Primaries (*P.*).—As a reference to the figure will show, these have now attained considerable dimensions, probably sufficiently to serve on occasion the purposes of flight.

Cubitals (*C.r.*).—The most proximal remiges have just pushed beyond the post-axial margin of the wing, whilst, as will be seen in fig. 3, the first remex of the series (the most distal) is about equal in length to its major covert; the rapid decrease in length of these remiges from 1 backwards is well seen in the figure, where only four remiges can be traced.

Tectrices :—

T. majores.—The dorsal row of these coverts (Pl. XI. fig. 3, *C*), like the remiges, is much further developed on the manus than on the cubitus.

T. mediæ.—Just appearing on the hand and distal portion of the forearm. The under surface of the wing is sparsely clothed with long slender neossoptiles, but gives no further evidence of the definitive feathers.

III. *Structure of the Neossoptiles and Plumulæ.*

Neossoptiles (Pl. XI. fig. 5, *N.*).—These are umbelliform, each consisting of some 15 rami, bound closely together at their base and continuous below with the definitive feather which it represents; there is, as the term umbelliform implies, no rhachis, and not even, as is often the case, a calamus or quill. These rami are produced into long filaments, which

extend beyond the most distal radii. Under a high power of the microscope (Pl. XI. fig. 6) the radii are seen to be composed of a series of flat lamellæ, or strap-shaped rods, joined end to end, and decreasing from the base upwards; the upper and lower margin of each radial segment are produced into a very delicate filum* or thread. These fila decrease in length towards the tip of the radius. The radii are of a nut-brown colour, the pigment being distributed in granules.

Plumulæ.—The plumulæ—the true nestling-down in this case—which develop towards the end of the nestling period, differ from the neossoptiles in that the rami are more numerous, forming thick brush-like tufts, and are not far produced beyond the radii. Microscopically the radii are found to be longer than in the adult plumulæ, and fila occur sporadically and rarely.

Rhamphotheca.—The cone-shaped elevations on the inside of the rhamphotheca described in the adult (p. 352) can be traced in all the nestlings, but not without difficulty in stages 1 and 2.

IV. *Pterylosis of the Embryo.* (Pl. XI. fig. 4.)

The pterylosis of the embryo presents us with two distinct phases. Stage 1 was kindly contributed by Prof. Newton, and roughly corresponds with a 5–6-day chick embryo. Here we have almost the earliest trace of feathers, which appear as small papillæ, mapping out the pterylæ as seen in the adult. The lower portion of the spinal and femoral tracts are somewhat imperfectly preserved; hence I cannot be so certain as I could wish as to their *precise* form, but I believe I have interpreted these parts correctly.

* I propose to substitute the word filum in future in place of "cilium;" the special sense in which this latter word is now employed renders its use in connection with feathers objectionable. I cannot lay claim, however, to the credit of this renaming; for, having brooded long and ineffectually upon the point, I at last consulted Dr. Benham (Aldrichian Demonstrator of Comparative Anatomy), and he helped me out of my difficulty by suggesting the highly appropriate term "filum."

In stage 2 the region immediately in front of and surrounding the sternal callosity, as also that portion of the apt. mesogastræi below this callosity to the umbilicus, bears long filaments representing either down- or contour-feathers, but these apparently disappear before hatching. The pt. spinalis is continuous with the pt. femoralis, the two fused tracts extending backwards to the tail. The apterium behind and below the external ear is relatively larger than in the nestling or adult, since it seems to extend for a short distance down the neck.

The conditions obtaining in this second stage seem to contradict what we find in the earlier embryo, nestling, and adult, inasmuch as the *apt. mesogastræi* is very narrow and gives promise of being clothed with either definitive or down-feathers; the spinal and femoral tracts occupy a larger area and are confluent, and the space below the external ear extends down to the neck. I am inclined to consider that the embryo feathers on the *apt. mesogastræi* should be regarded as representing definitive rather than down-feathers, in that, these excepted, there are no traces of down-feathers visible on the body; the down-papillæ having now sunk below the surface, the feather itself will not make its appearance till after incubation.

Rhamphotheca.—In some of the older embryos the conical elevations on the inner side of the rhamphotheca (p. 356) can be plainly discerned; in addition, I find on the tip of both upper and lower jaws a remarkable papillated pad, which I propose to submit to a careful microscopic examination, the results of which I shall submit to the readers of 'The Ibis,' together with some other observations on the tooth-like structures on the rhamphotheca of the nestling Tinamou described in my last paper ('Ibis,' 1895, p. 1).

Let us now collect and analyze such of the foregoing statements as will enable us to express briefly the chief characteristics of the pterylosis of *Opisthocomus,* as well as those which appear to be new in connection with the present paper.

The main features about the pterylosis of *Opisthocomus*

appear to me to be that the feathers are remarkably few and sparsely distributed; as a natural consequence the pterylæ are but feebly defined.

The contour-feathers, as already pointed out, are characterized by their comparatively great length and freedom from downy rami at the base; further, they are somewhat harsh to the touch and coarse in structure, a feature which my readers will recall as characteristic of certain *Cuculidæ*, e. g. *Centropus*.

V. *Systematic Position of* Opisthocomus.

As to the systematic position of *Opisthocomus*, as indicated by its pterylosis, I had rather not express an opinion yet, for the very good and sufficient reason that I do not possess sufficient reliable data. Nitzsch's is really the only work of reference, and I have lately found so many of his figures incorrect that it seems to me unwise to waste time in making comparisons which depend upon the accuracy of this author's figures for their value.

Quite recently Mr. Beddard has generously provided me with a collection of *Cuculidæ* and *Musophagidæ*, and when I have carefully examined all these I propose to present the readers of 'The Ibis' with a brief summary of the result. There then remains to be worked out the pterylosis of the obviously more closely related *Galli* and the *Rallidæ*. To postpone the publication of the present paper until all this has been done seems to me unwise, especially since it probably would nearly double its bulk. We might, however, with some profit perhaps, run through the most noticeable points in the pterylosis of *Opisthocomus*, so as to bring out, as far as is possible, those in which it agrees or disagrees (1) with the *Galli* and (2) with the *Cuculi*, and also certain Ralline affinities which have been ascribed to this bird. Thus, then, *Opisthocomus* agrees with the *Galli* in that the wing is quintocubital, in the remarkable order of the development of the metacarpo-digital remiges (primaries), and in that the number of these remiges is 10. With the *Cuculi* there is a striking general resemblance in the ptery-

losis and in the distribution of the feathers of the spinal tract in particular. Thus, in *Turacus* and *Centropus*, for instance, the pt. spinalis has run down and fused with the pt. femoralis, whilst in *Opisthocomus* that portion of the apt. trunci lateralis dividing these tracts is sparsely covered with both down-feathers and semiplumes. Now it seems to me that these semiplumes are to be regarded as degenerated contour-feathers*, as was suggested long ago by Garrod (see p. 366), the evident remains of a once continuously feathered area. Again, there is a striking similarity in the pterylosis of the wing of *Turacus* and *Opisthocomus*. We may count as Ralline†, or perhaps Gruiform, the structure of the "neossoptiles" (p. 355), since this agrees precisely with that of *Crex*, for instance, but is entirely different from the Galliform neossoptile, with its well-developed rhachis and aftershaft. The presence of down both on the pterylæ and apteria is another Gruiform character. The position of the external nares might, perhaps, be taken into consideration here—if it have any weight at all. But, in that we can divide the nestling-plumage into neossoptiles and plumulæ, *Opisthocomus* appears to be unique. This is a matter, however, for further investigation, though up to the present plumulæ have never been described as forming part of the plumage of the nestling, which has always been supposed to consist of neossoptiles ("nestling-down") only.

The nestling makes up for any lack of novelty that may be deemed to be wanting in the adult.

The young of *Opisthocomus* are nidifugous, and, as we have already seen, sparsely clothed in a covering of fine down, which, in its thickness, would seem to be somewhat intermediate between that of the Pigeon on the one hand and the Fowl or Rail on the other. This downy covering is formed in the same place as the future definitive feathers. Dr. Gadow has recently aptly named these "nestling down-"

* The conditions which obtain at a certain stage of development in the embryo tend to support this view (see p. 363).

† I speak guardedly here, as I have not yet had an opportunity of examining a series either of nestlings or adults of this group.

feathers "neossoptiles." In addition to this covering of neossoptiles, there is developed towards the end of the nestling-period a second downy covering, which, for a time, bears a considerable share—if not the greater part—in clothing the bird. This second downy covering is composed of true down-feathers or plumulæ, and, so far as I am aware, such a covering has never before been described in any nestling.

In the wing of the nestling we have a revelation of profound importance, for, so it seems to me, through it we get a glimpse into the phylogeny not only of its immediate allies, the *Gallinæ*, but possibly of the whole avian class.

The first step in the direction of this discovery was made by Mr. Quelch (12) when he found that the nestling of *Opisthocomus* used its wings to assist it in climbing about the trees in which its nest was placed. In a most valuable and interesting paper he details with great clearness the wonderful life-history of these birds. Suffice it here to say that *Opisthocomus* is arboreal in the strictest sense of the word, since it rarely, if ever, descends to the ground; hence the enormous feet and sternal callosity. Nidification is performed in trees, apparently those overhanging the water for preference. As I have already elsewhere written (11), "the young . . . . instead of remaining in the nest until they are able to fly, are in the habit, at a very early stage in their life, of climbing out of the nest, it may be to gain a better coign of vantage whence to meet the parents returning with food, or to take refuge in more dense foliage to escape an enemy—sometimes the one and sometimes the other cause impels them to leave their home; in either case it is obvious that the chances of a fall are exceedingly probable. Now, as might have been expected, these youngsters are particularly capable of taking care of themselves, possessing not only enormous feet fitted for grasping—like the parents—but they have powerful auxiliaries in the shape of the beak, which is used much as is that of a Parrot in climbing, and wings, which are armed with large claws on the first and second digits. On turning to fig. 2, p. 361, it will be seen that the general form of the wing renders such a mode of

Fig. 2.

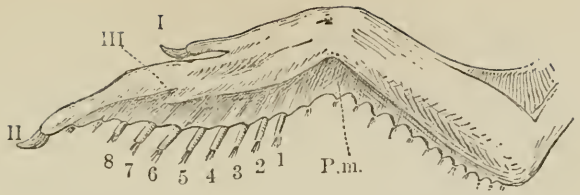


Fig. 2.—The right wing of a nestling *Opisthocomus cristatus*, ventral view, showing how that the 2nd digit (II.) is produced beyond the ala membrana (P.m.), and that the development of remiges 8–10 has been arrested, so as not to interfere with the freedom of the long finger when climbing.

Fig. 3.

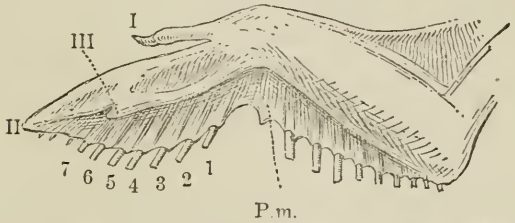


Fig. 3.—The right wing of a nestling of a Common Fowl (*Gallus bankiva*), an ally of *Opisthocomus*. Owing to the exchange of an arboreal for a terrestrial habit, the manus is gradually shortening. The pollex only retains the claw. The 2nd digit projects but slightly beyond the ala membrana; but the development of the most distal remiges is still arrested.

Fig. 4.

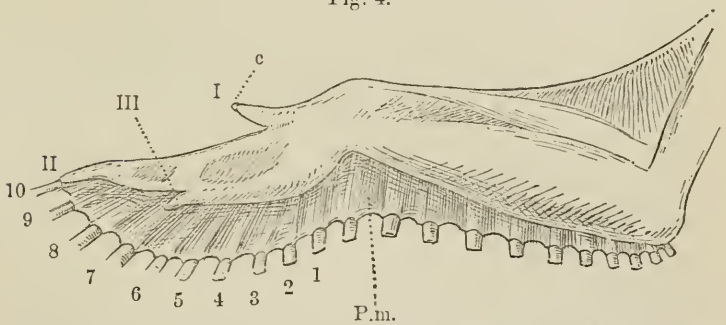


Fig. 4.—The right wing of an adult *Opisthocomus cristatus*, ventral view. Contrast with that of the young bird, and the manus will be found to be shorter than the forearm; the "pollex," or "thumb," is considerably reduced, as is also digit II. The claw may be seen on the pollex as a slight wart (*c*). 1–10. Metacarpo-digital remiges, or quill-feathers; P.m. Ala membrana, or posterior wing-membrane; *c*. Claw.

All the figures (2, 3, and 4) are original, and were drawn by the writer from the actual specimens. They have been kindly lent to this Journal by the Editor of 'Natural Science.'

locomotion quite probable, and may therefore be said to entirely corroborate Mr. Quelch's statements. The hand is considerably longer than the forearm, the pollex or thumb extends beyond the level of the tip of the 3rd digit, and is provided with a large claw; the 2nd digit, with an equally large claw, is produced beyond the fold of skin running along the posterior border of the wing, which encloses the base of the quills. Of these, it will be noticed, only 1–8 have extended any distance beyond the wing-fold just mentioned, so that a long free finger-tip is left. As the bird grows and the feathers develop, the proximal ones grow faster than the distal, so as not to impede the freedom of the hand in climbing; but as soon as the proximal feathers have increased sufficiently to serve to break the force of a fall, should such occur, the remaining distal feathers begin to develop; at the same time the hand begins to shorten till, as will be seen in fig. 4, p. 361, in the adult, the hand has become *shorter* than the forearm, the claws have disappeared, the thumb no longer extends to the level of the 3rd digit, nor does the 2nd project beyond the posterior wing-fold, the bird now being able to move from one place to another by flight instead of by climbing."

Should a nestling by any chance fall into the water, it seems that it is able to save itself by swimming, since Mr. Quelch tells us that on one occasion, happening to drop a youngster from a boat into the river, it immediately dived out of reach; coming to the surface a yard or so further on, it again dived, and finally escaped by gaining the shore and disappearing among the herbage.

It is not improbable that the life-history of *Opisthocomus* is a survival of what was at one time shared by the *Galli*, since in nestlings of *Cracidæ* and *Gallidæ* the wing exhibits precisely the same phenomena as we have just noticed in *Opisthocomus*; the details, however, are not quite the same, inasmuch as in *Opisthocomus* we have an order of things at their maximum development, whilst in the *Gallidæ* and *Cracidæ* we have the same order in its decline, and responding to the demands of a changed environment.

In the wing of the nestling of *Crax*, the Common Fowl

(fig. 3, p. 361), and the domestic Turkey, I find that remiges 1–7 have attained a considerable degree of development, while the three distal remiges are as yet only represented by neossoptiles; thus, as in *Opisthocomus*, a free finger-tip is left. The exchange, however, of a terrestrial for an arboreal habit has brought about an exaggeration of one feature whilst it is eliminating others, inasmuch as an accelerated development of the metacarpo-digital remiges has plainly taken place, whilst the once long hand is being gradually shortened; the manus, however, is still (11) "longer than the forearm, ... but the 2nd digit is scarcely produced beyond the wing-membrane, and the claw has been lost, though present in the embryo, the pollex has retained the claw and extends just up to the 3rd digit."

The accelerated development of the metacarpo-digital remiges, just referred to, can best be understood by a comparison of fig. 3, p. 361, representing the wing of a nestling Fowl, with that of *Opisthocomus* (stage 5), Pl. XI. fig. 3. A glance will serve to show that while in *Opisthocomus* all the remiges are represented by definitive feathers, and whilst there is a perfectly easy gradation in the length of the same from within outwards, the terminal feather being the smallest of the series, in that of the Fowl there is an abrupt change from definitive feathers to neossoptiles, the change taking place directly after the 7th remex.

It seems probable that these remiges have undergone what we might describe as a process of forcing—or, as I have already called it, accelerated development—in which the proximal remiges have developed at an excessively rapid rate, so as to out-distance their fellows at the distal extremity of the wing, which are as yet only represented by neossoptiles. The rapid development of these seven remiges is probably due to the fact that the terrestrial mode of life demanded the aid of the wings for the purposes of flight at an earlier period than would be the case if they still dwelt, like *Opisthocomus*, in comparative security amongst the trees. According to this theory the function of the claw of digit II. begins to wane as soon as the distal remiges project beyond

its tip; and if so, it may be asked: Is the wing-area at this stage sufficient in the case of *Opisthocomus* to transform a fall into flight, or in the Fowl, having approximately the same wing-area, to enable it to rise from the ground if pursued by an enemy? By way of answer I would refer to Pettigrew's experiments (10) on flight made upon the Common Sparrow. Of one of these he writes, "Detached the half of the secondary feathers and a fourth of the primary ones of either pinion in the long axis of the wing. Flight in no wise impaired." Again, "Detached rather more than a third of both primary and secondary feathers of either pinion in the long axis of the wing. In this case the bird flew with evident exertion, but was able, notwithstanding, to attain a very considerable altitude." As a result of his experiments he came to the conclusion that "the wing-area is, as a rule, considerably in excess of what is actually required for the purposes of flight." The wing-area of the first of these two experiments which I have quoted seems to correspond roughly to that which obtains in the nestling *Opisthocomus* (Pl. XI. fig. 3) (stage 5) and of the Fowl (Pl. XI. fig. 1), and thus serves to support my interpretation of the somewhat puzzling facts we have been discussing.

Finally, in connection with this subject, I would draw the attention of my readers to the fact that in the *Galli* the remiges developed during the nestling period are replaced by others before the bird has quite reached maturity, whilst usually the original remiges are retained during the first year of life. Now, so far as I know, we are yet in ignorance as to whether (1) *all* the remiges are so replaced, or whether (2) the distal (mid-digital and pre-digital) remiges, and perhaps even the cubitals, are retained.

A more careful investigation of this point may possibly, by revealing new facts, show that the theory of the supposed sometime arboreal habits of the *Galli*, based upon the evidence of the development of the remiges, will have to follow many more of its kind into the land of oblivion; at any rate it will have played a good part if only by serving to stimulate a search after the real explanation.

VI. *Literature of the Pterylosis of* Opisthocomus.

Let us now turn to the literature of the subject. Happily this is not extensive.

Nitzsch was, I believe, the first to describe and figure the pterylosis of *Opisthocomus*. On examining his figure we find the bare, brightly-coloured skin on the sides of the face represented as if restricted to a relatively small area, partly surrounding the eye from below. The spinal tract starts, he tells us, "as a strong triserial band* from the midst of the plumage of the lower part of the neck, and divides between the shoulders into two limbs, with which the originally divergent feather-rows of the biserial hinder part are united at the end; from the caudal pit onwards it becomes somewhat broader, and encloses the oil-gland." The ventral tract, we are told, "commences as two broad bands, which run down close to the keel of the sternum, and become somewhat stronger at the outer margin. . . . . At the end of the sternum these are narrowed, and pass on, gradually becoming weaker, to the anus, at which they terminate with a breadth of only two feathers. . . . . In the wing there are nineteen remiges, of which ten are on the pinion."

The next reference to the pterylosis of *Opisthocomus* is that by Mr. J. B. Perrin (9), who, after an examination of some "spirit-specimens," seems to have persuaded himself that "the pterylography was almost identical with that figured in Nitzsch's work." As Mr. Beddard (1) has pointed out, the word "almost" in a question of pterylography "allows a considerable latitude for variation." Perrin has illustrated this portion of his paper with Nitzsch's figures, much enlarged, and not quite correctly copied.

The late Prof. Garrod (5), referring to Nitzsch's representation of the pectoral region of *Opisthocomus*, suggested that it was due to "an accidental error," and that he "evidently had an imperfect skin to work upon." He next describes the sternal callosity as "an oval area, about 0·75 inch long from above downwards, and 0·25 inch in breadth,

* Composed of three longitudinal rows of feathers.

of dense naked skin, covering the surface of the expanded upper cutaneous surface of the carina sterni." Further, he remarks, "*Opisthocomus* is one of those birds in which the pterylosis is not so decisive of its affinities as in many cases, the reason being that so great an amount of the unfeathered spaces is protected by semiplumes. May not these semiplumes in many instances be degenerated feathers? This question has never been decided, so far as I am aware."

In a somewhat extraordinary paper by Dr. C. G. Young (14), we gather the following statements as to the pterylography:— "The young is covered with a light coat of dark brown down." Of the adult he writes:—"The bill . . . . with black hairs at the base; . . . . the eyes . . . . have black eyelashes; the skin round them and on the neck is light blue, and immediately round the eye and on the sides of the head it is almost naked, having only black hairs and small feathers here and there."

"Both jaws have a row of tubercles on their inner margin that act as teeth. . . . . There is an atrophied nail on the top of the thumb and finger."

The wing of the nestling is described as "having the forearm longer than the arm, and the hand longer than the forearm. The thumb is long and well developed, and has a long well-developed claw; . . . . the point of the wing is tipped with a claw equal in size to that of the thumb; both the thumb and the finger have the power of ab- and adduction. As soon as the young escape from the egg they creep about with the assistance of these hands, stretching out their wings and digging these claws into, or hooking on to, whatever they meet . . . ."

Mr. Beddard (1) has written the most exhaustive account of the pterylosis of *Opisthocomus* hitherto published, commencing, as he does, with the adult and ending with the embryo.

In the adult, Mr. Beddard says, "the ventral surface is covered with a continuous feather-tract as far down as about halfway between the fore and hind limbs; after this there is a median bare space of some extent, which is, however,

sparsely feathered. The median *apterion* does not, in fact, commence until the carina sterni, and is here exceedingly narrow, its width being precisely that of the carina; the *apterion* is sharply marked here by a straight row of feathers on each side; from this point the *apterion* is conspicuous and of some breadth, and the two ventral tracts become narrow, though connected by scattered feathering with the femoral tracts.

"The lateral ventral tracts unite with one another some way in front of the cloacal aperture.

"The spinal tracts do not show quite so regular an *apterion* as in Nitzsch's figures; indeed, the dorsal surface is sparsely feathered all over, with stronger feathers here and there, particularly anteriorly, where they form a strong band, as figured by Nitzsch.

"The humeral tracts are conspicuous, as figured by Nitzsch.

"In the nestling the condition is much the same, but the down-feathers are more numerous."

In the embryo "the ventral *apterion* is as conspicuously developed as in the adult bird. . . . . On the dorsal surface the feathering appeared to be quite uniform, though sparse; in these young chicks the ventral feathering was much closer than the dorsal."

Dr. Gadow (3) briefly refers to the pterylosis of *Opisthocomus* as follows:—"Dunen auf den Rainen und zwischen den Conturfedern. Der ganze Hals ist befiedert, ohne Seitenrain. Unterflur von der Brust an getheilt, jederseits breit beginnend, ohne Aussenast, allmählich zum After zusammenrückend und sich verschmälernd. Dorsalflur zwischen den Schultern aus jederseits zwei Reihen Federn bestehend, und undeutlich gespalten, dann als schmaler, nur zwei Federn breiter Streif, ohne Andeutung von Sattel bis zur Bürzeldrüse gehend."

Later the same author writes (4), "Die Jungen . . . . sind mit einem spärlichen gebauten. . . . . Erstlingsgefieder bedeckt," and again, "bei den erwachsenen Dunen spärlich auf den Rainen und zwischen den Conturfedern stehen und

dass besonders auf den Rainen viele zu Fadenfedern umgewandelte Dunen vorhanden sind.

"Die Zahl de Schwungfedern beträgt 10 Hand- und 9 Armschwingen; von letzteren ist die fünfte vorhanden. . . . . Der Hals ist ganz befiedert, ohne Seitenraine."

Nitzsch's description and figures of the pterylosis of *Opisthocomus* are, as has been pointed out by other writers, somewhat faulty; such of his statements that I find myself unable to agree with I have quoted at the beginning of this section of my paper.

As touching the pterylosis of the head, I have already hinted that this is too densely feathered in his figure. The spinal tract in my specimens terminates in *front* of the oil-gland, and does not expand or surround it. The ventral tract, as earlier writers have pointed out, is wrongly represented as dividing at the base of the neck, whilst, as we have seen, this division actually takes place about midway between the fore and hind limbs. Nitzsch committed a much more serious error when he represented *Opisthocomus* as possessed of clavicles and a long carina sterni; a fact which, to my mind, seems to prove that this author's figures were drawn from a skin, in which case, as Garrod has suggested (5), if he had never dissected this bird, he could scarcely have been expected to divine the extraordinary development of the crop and the consequent modification of the sternum which has followed, from an inspection of the pterylosis; the fact that the sternal callosity is not indicated in his drawing seems a further proof, for in the dried skin this would probably suggest nothing more to his mind than the scar of some old wound.

I find the apterium spinale wider and more sharply defined than is indicated in Nitzsch's figure, while the tract, instead of expanding and enclosing the oil-gland, terminates as a double row of feathers in front of that gland. I find 11 cubital remiges.

One of the most interesting of Garrod's (5) observations on this subject is the suggestion that the semiplumes clothing the "unfeathered spaces" might represent degenerated

contour-feathers. There seems to be very good reason for believing this may be really the case. In the nearly ripe embryo, it will be remembered, the pt. spinalis and femoralis appear to be confluent, whilst in the adult, as a reference to the figures (Pl. IX.) will show, the actual distribution of the contour-feathers in this region has become much restricted. The semiplumes distributed in the space dividing the femoral from the spinal tract probably represent degenerate contour-feathers. It remains to be seen whether, on examination of perfectly fresh specimens, these semiplumes correspond to the embryonic feathers in the same region. In my specimens many of these feathers (semiplumes) have been lost, so that it is difficult, if not impossible, to settle this point now.

Mr. Beddard's paper (1) contains one or two statements which I cannot entirely corroborate. As touching the spinal tract, for instance; although in the spirit-specimens the pt. spinalis is not so sharply defined as in my figures, inasmuch as there are no boundary lines, such as I have drawn, yet we can scarcely say that the "dorsal surface is feathered all over with larger feathers here and there." Again, as touching the "median apterion" (*apt. mesogastræi*). In my adult specimens this is certainly not "sparsely feathered," nor can it be said that the "median apterion does not . . . . commence until the carina sterni, ... its breadth being precisely that of the carina." The nestlings, however,—and the nearly ripe embryo—seem to support Beddard's statements; but in how far this is actually the case remains to be seen, inasmuch as it is an almost hopeless task to differentiate between down-feathers (*plumulæ*) and neossoptiles with anything like precision enough to settle the question, and hence this must be left for a further examination of freshly-killed specimens. It is quite possible that, these being small and probably semiplumous feathers, they have fallen out in the adult submitted to me. I do not find that the lateral ventral tracts unite with each other in front of the cloacal aperture, or that they are connected with the femoral tracts by scattered feathering.

In the nestling Beddard almost distinguishes between the

neossoptiles and true nestling down-feathers (plumulæ), in that he remarks that the "down-feathers are more numerous" than in the adult.

Of the embryo it is stated that "on the dorsal surface the feathering appeared to be quite uniform, though sparse; there was no distinct spinal apterion." The figure accompanying this description was drawn from a stage apparently roughly corresponding to that of a 5–6-day chick embryo. From a specimen apparently a few hours older (Pl. XI. fig. 4), kindly furnished by Prof. A. Newton, I find an undoubtedly distinct spinal apterium, but, as I have already remarked, the precise form and limits of the pt. spinalis and pt. femoralis could not be positively determined. In justice to Mr. Beddard I should mention that this embryo was a better preserved specimen than that which he described.

Dr. Gadow describes the branches of pt. ventralis as gradually approaching each other, and at the same time decreasing in width, whilst, according to my specimens, the branches do not decrease, but *increase* as they approach the cloacal aperture. I have not found anything to support the statement that much of the down upon the apteria has become transformed into filoplumes. The actual number of cubital remiges is 11, not 9.

In conclusion I wish to tender my thanks to Dr. Sclater for having so kindly entrusted me with this investigation, and to express a hope that ere long fresh material will come to hand, so as to enable us to set at rest one or two little matters of detail that I have been unable to settle with certainty in the present paper.

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EXPLANATION OF THE PLATES.

(All the figures are original.)

Plate IX.

Fig. 1.—Dorsal aspect of an adult *Opisthocomus*, showing the arrangement of the pterylæ. The shaded parts represent the apteria. The relative sizes of the feathers are indicated by large and small dots.

Apt.a.sup.	Apterium	alæ superius.
Apt.cap.	,,	capitis.
Apt.t.lat.	,,	trunci laterale.
Apt.sp.	,,	spinale.

Pt.c.	Pteryla caudalis.
Pt.cap.	„ capitis.
Pt.coll.	„ colli.
Pt.cr.	„ cruralis.
Pt.f.	„ femoralis.
Pt.h.	„ humeralis.
Pt.sp.	„ spinalis.
Pt.u.	„ uropygii.
P.	Parapteron.
U.	Uropygium.

Fig. 2.—Ventral aspect of same, showing the arrangement of the pterylæ. The shaded parts represent apteria.

Additional Letters.

Apt.t.lat.	Apterium trunci laterale.
Apt.m.	„ mesogastræi.
Pt.a.	Pteryla ani.
Pt.v.	„ ventralis.
St.cal.	Sternal callosity.

Fig. 3.—Right-side view of same. The shaded parts as before.

Additional Letters.

Apt.a.inf.	Apterium alæ inferioris.
H.	Hypopteron.

Plate X.

Fig. 1.—Dorsal aspect of a nestling *Opisthocomus cristatus*, showing the arrangement of the pterylæ. The shaded parts represent the apteria.

Letters as in Plate IX.

Fig. 2.—Ventral aspect of the same. The very small dots are intended to indicate approximately the distribution of the plumulæ or down-feathers.

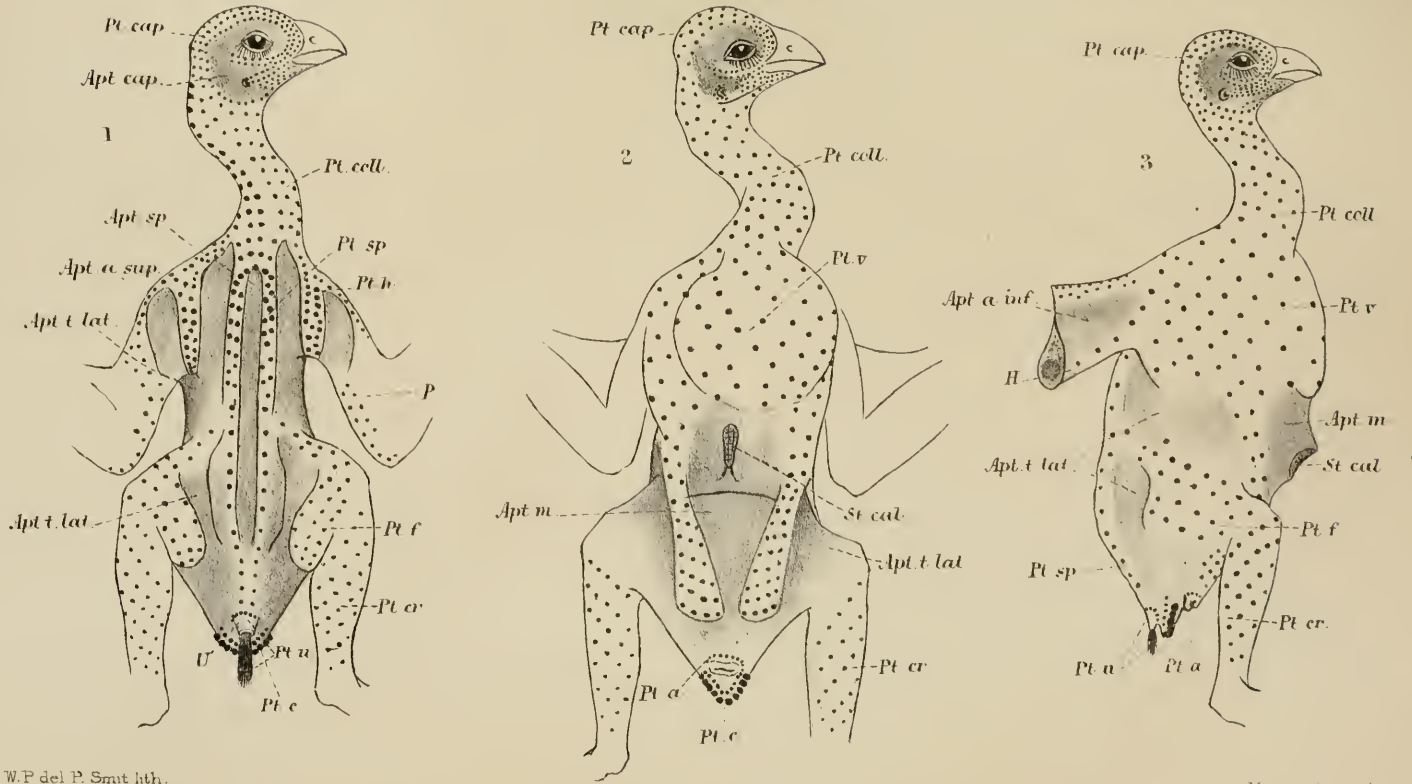
Um. Umbilicus. Other letters as in Plate IX.

Fig. 3.—Right side of the same. The small dots, as in fig. 2, indicate the distribution of the plumulæ.

Letters as before.

Plate XI.

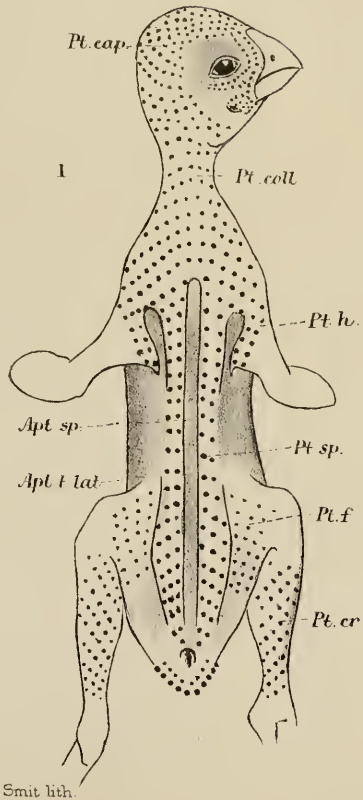
Fig. 1.—Left wing of a nestling of the Common Fowl, dorsal view, showing how, whilst the development of the proximal metacarpo-

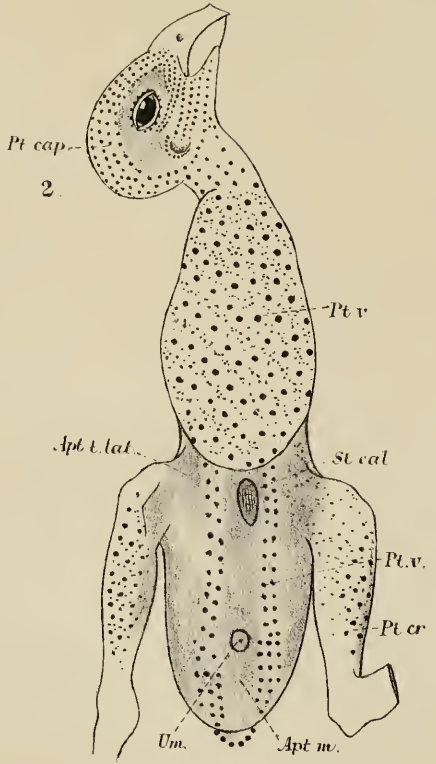


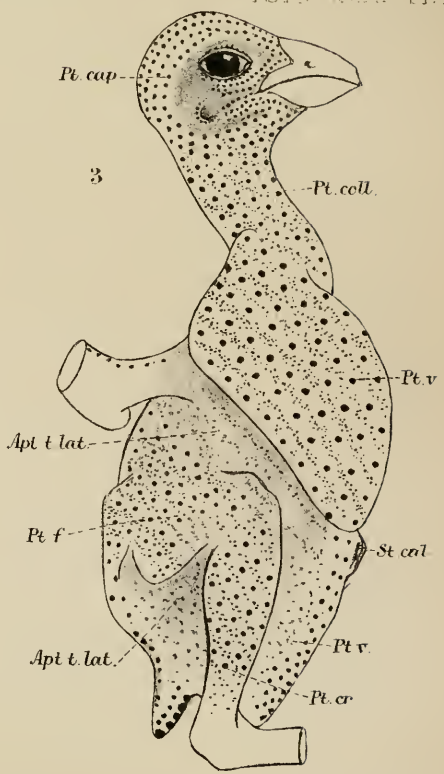
W. P. del P. Smit lith.

PTERYLOSIS OF OPISTHOCOMUS CRISTATUS.

Mintern Bros. imp







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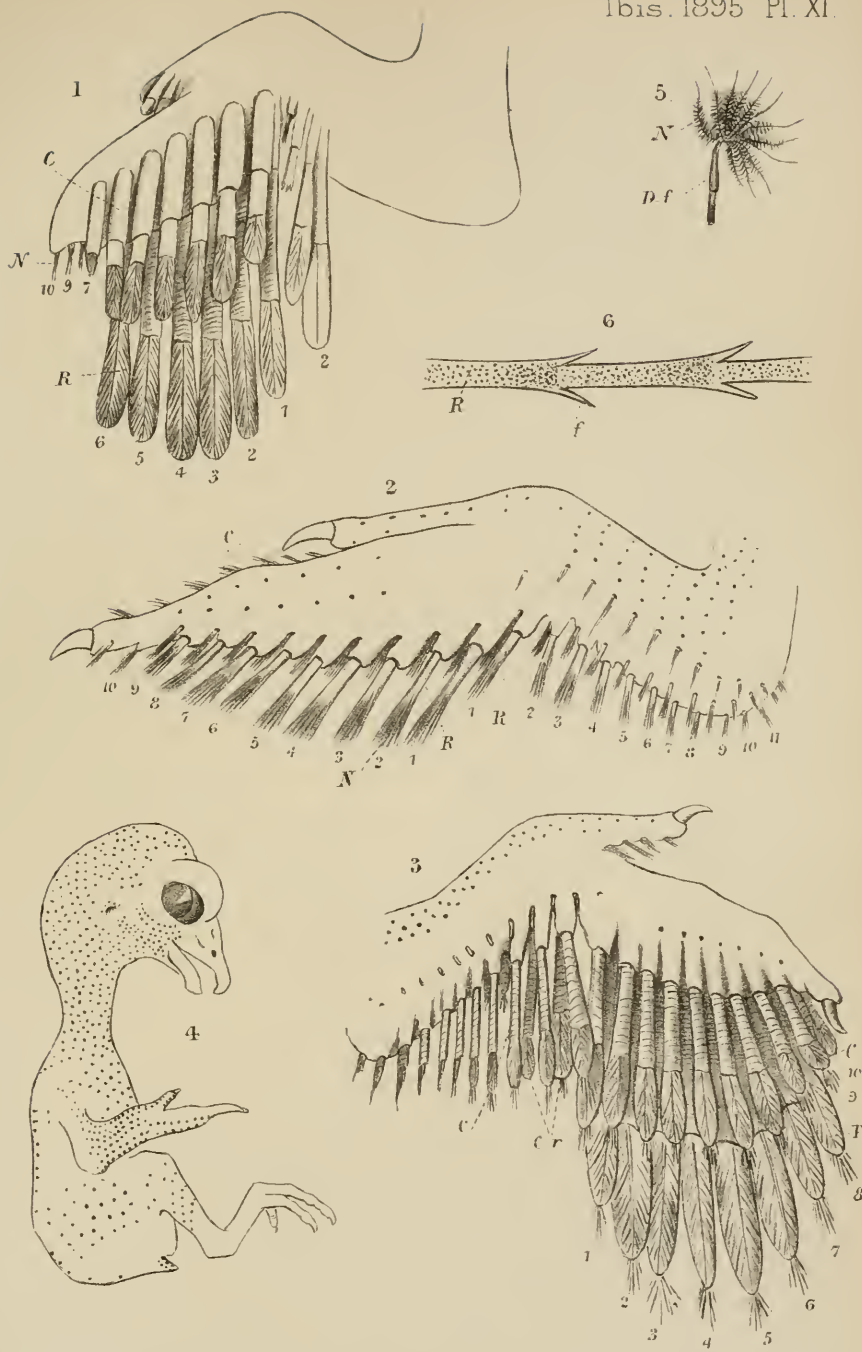
PTERYLOSIS OF OPISTHOCOMUS CRISTATUS.

Mintern Bros. imp.



W.P. del. P. Smit lith. Mintern Bros. imp.

PTERYLOSIS OF OPISTHOCOMUS CRISTATUS.

digital (primary) remiges (*R.*) has become much accelerated, that of the distal remiges (*N.*) has been arrested *pro temp.*, thus leaving a free finger-tip, sometime functional in the past history of the species.

C. Coverts. *N.* Neossoptiles.

Fig. 2.—Left wing of a nestling *Opisthocomus*, showing the arrested development of the distal remiges, leaving a free finger-tip, functional at the present day, enabling the bird to climb before the power of flight is acquired.

Fig. 3.—Right wing of a nestling *Opisthocomus*, older than that represented in fig. 2. Here the finger-tip has almost, if not quite, ceased to be functional; the primaries being now capable of sustaining flight.

C. Coverts. *Cr.* Cubital remiges. *P.* Primaries.

Fig. 4.—Embryo *Opisthocomus*, showing the feather-papillæ, the "fundaments" of the future definitive feathers.

Fig. 5.—A neossoptile (*N.*) of *Opisthocomus* on the tip of a definitive feather (*D.f.*), natural size.

Fig. 6.—Portions of a radius (*R.*) of fig. 5, highly magnified, showing fila (*f.*).

XXIX.—*Further Notes on Birds from Bugotu, Solomon Islands, with Description of a new Species.* By H. B. Tristram, D.D., LL.D., F.R.S.

I have lately received, through my friend Dr. P. H. Metcalfe, of Norfolk Island, a small additional collection of birds made for me by Dr. Welchman on Bugotu, one of the lesser islands of the Solomon group*. The collection consists of 14 specimens referable to 12 species, some of which are of considerable interest, though many are well known. The native names are attached to the specimens, and these, except in one or two instances, bear little resemblance to the names given in Guadalcanar, which again differ altogether from

* See previous paper, Ibis, 1894, p. 28.